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ORIGINAL PAPER

Changing roles of propagule, climate, and land use during extralimital colonization of a rose chafer beetle

Jakub Horak · Cang Hui · Núria Roura-Pascual · Dusan Romportl

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Abstract Regardless of their ecosystem functions, some insects are threatened when facing environmental changes and disturbances, while others become extremely successful. It is crucial for successful conservation to differentiate factors supporting species' current distributions from those triggering range dynamics. Here, we studied the sudden extralimital colonization of the rose chafer beetle, *Oxythyrea funesta*, in the Czech Republic. Specifically, we depicted the range expansion using accumulated historical records of first known occurrences and then explained the colonization events using five transformed indices depicting changes in local propagule pressure (LPP), climate, land use, elevation, and landscape structure. The slow occupancy increase of *O. funesta* before 1990 changed to a phase of rapid occupancy increase after 1990, driven not only by changes in the environment (climate and land use) but also by the spatial accumulation of LPP. Climate was also found to play a significant role but only during the niche-filling stage before 1990, while land use became important during the phase of rapid expansion after 1990. Inland waters (e.g., riparian corridors) also contributed substantially to the spread in the Czech Republic. Our method of using spatially transformed variables to explain the colonization events provides a novel way of detecting factors triggering range dynamics. The results highlight the importance of LPP in driving sudden occupancy increase of extralimital species and recommend the use of LPP as an important predictor for modeling range dynamics.

Keywords Climate change · Local propagule pressure · Occupancy · *Oxythyrea funesta* · Population dynamics and establishment · Riparian corridors

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J. Horak (✉)
Faculty of Forestry and Wood Sciences,
Czech University of Life Sciences Prague, Kamycka 1176,
16521 Prague 6, Czech Republic
e-mail: jakub.sruby@gmail.com

C. Hui
Centre for Invasion Biology, Department of Botany and Zoology,
Stellenbosch University, Matieland 7602, South Africa

N. Roura-Pascual
Àrea de Biologia Animal, Departament de Ciències Ambientals,
Facultat de Ciències, Universitat de Girona, Campus Montilivi,
17071 Girona, Catalonia, Spain

N. Roura-Pascual
Landscape Ecology Laboratory, Centre Tecnològic Forestal
de Catalunya, Crta. de Sant Llorenc de Morunys Km. 2,
25280 Solsona, Catalonia, Spain

D. Romportl
Department of Physical Geography and Geoecology,
Faculty of Sciences, Charles University, Albertov 6,
12843 Prague, Czech Republic

Introduction

Human-mediated changes in climate and land use can have profound effects on species' survival and distribution (Lepers et al. 2005; Thomas et al. 2004; Both et al. 2006; Roura-Pascual et al. 2011). While most species are dwindling due to these changes—especially specialists or rare species, others behave rather robustly with some even thriving in the novel environment created by these changes (Samways 2007). Indeed, many introduced and indigenous species, which were previously constrained by dispersal and ecological barriers, have been reported to rapidly change the distributional structures of their novel or historical ranges (e.g., undergoing rapid range expansion; Richardson and Pyšek 2006; Konvicka et al. 2003; Roura-Pascual et al. 2009). It is, thus, crucial for any

successful conservation effort to examine what factors trigger and drive the dynamics of species occupancy and distribution (i.e., expansion or retraction; Lockwood et al. 2005; Soberón and Peterson 2005).

The extralimital colonization of many indigenous species, to this end, provides an ideal natural experiment for clarifying the triggers and drivers of the rapid spread of those species with a previously rather static distribution. Compared to many invasive alien species whose range expansion represents the process of filling existent empty niches (Lockwood 1993; Ricklefs 2010), extralimital species (i.e., domestic exotics) can colonize either by filling novel niches created by environmental changes (Guo and Ricklefs 2010) or outburst due to accumulating local propagule pressure (LPP; i.e., the accumulation of individuals dispersed from viable surrounding populations determines the colonization success of an empty habitat; Lockwood et al. 2005). We, therefore, expect to identify both habitat characteristics and LPP as important drivers of extralimital colonization.

As a species-rich taxon with important ecosystem functions, insects often respond to environmental changes in various ways (Samways 2007; Horák et al. 2012). Some insect species become enormously successful when facing environmental changes and take great advantage of habitats created by changes in climate (Parmesan 2006; Rosenzweig et al. 2008) and land use (Zimmermann et al. 2005). Some habitat specialists and other endangered fauna can even thrive in highly disturbed habitat remnants (Beneš et al. 2003; Tropek et al. 2010; Lenda et al. 2012). This leads to a common phenomenon that retracting species are often associated with, although not necessarily caused by, expanding extralimital species in human-modified environments.

To date, quantitative studies on the role of LPP during a sudden and rapid colonization event of a rare species are lacking. We here examine both the buildup of LPP and environmental gradients that could potentially drive the sudden extralimital colonization of the rose chafer beetle *Oxythyrea funesta* (Poda 1761; Coleoptera: Scarabaeoidea: Cetoniidae), an important pollinator at adulthood and scavenger at larval stage. Besides its widespread Palearctic distribution, *O. funesta* has been considered rare and near extinction in the Czech Republic (Král 1989). We propose a unique way to quantify LPP and its role in triggering the sudden fast colonization of *O. funesta* in the last decades. Specifically, we first identify the transition time between the slow and fast phases of extralimital colonization and then seek for key drivers of colonization among LPP and environmental factors for both before and after the transition time. Our study, thus, highlights the changing role of environmental factors at different stages of colonization.

Materials and methods

Study species and area

Eleven species are known from the genus *Oxythyrea* Mulsant 1842. The rose chafer beetle *O. funesta* is the only species that distributes throughout Europe and partly in northern Africa and Asia (Smetana 2006). It has a 1-year development time, with larvae developing in decaying residues and overwintering adults feeding on pollens of many plant species. This species has been considered a rare thermophilic relict of postglacial steppes occurring in scattered patterns on xeric localities in most central European localities (Horion 1958; Burakowski et al. 1983), although it has recently undergone a sudden colonization and thus become an extralimital invader (Guo and Ricklefs 2010).

We here study the colonization event of *O. funesta* in the Czech Republic under temperate continental climate (Tolasz 2007). This central European country has recently started to experience rising temperatures and changing rainfall patterns (Kyselý 2004; Dubrovský et al. 2005) and also witnessed a dramatic change in land cover after World War II when socialist industrialization (1948–1989) gradually transformed large extensions of grasslands into agricultural land and subsequently into industrial zones (Krahulec et al. 2001). This trend of land use changes has been further altered since the Velvet Revolution in 1989 when the use of fertile land started to intensify due to the competition of Czech agriculture and forestry with other EU states, with unproductive areas gradually being converted back to grasslands or commercial forests (Bičík et al. 2001).

Occurrence and environmental data

Species occurrence data in the study area were excerpted from published sources (Table S1) and an online database (Chobot and Horák 2012; $n=675$ records from 1819 to 2010). All data were mapped in the rectangular Central European grid cell system, with a resolution of 10′ longitude by 6′ latitude (equivalent to 11.1×12 km) and a total of 676 grid cells in the Czech Republic (Fig. 1). Occurrence data were not derived from an annual systematic survey (see Rocchini et al. 2011), so most grid cells recorded the presence of the species more than once within 1 year or for multiple years. For grid cells with more than one record of presence, we used the oldest records to represent the first occurrence ($n=299$).

These records of first occurrences were then used (1) to detect the transition time of the two-phase colonization (a slow occupancy increase followed by a fast increase) by plotting the occupancy based on first occurrences over time and (2) to identify key factors driving the colonization at different phases (i.e., for the slow and fast colonization periods, respectively) by means of a multivariate analysis.

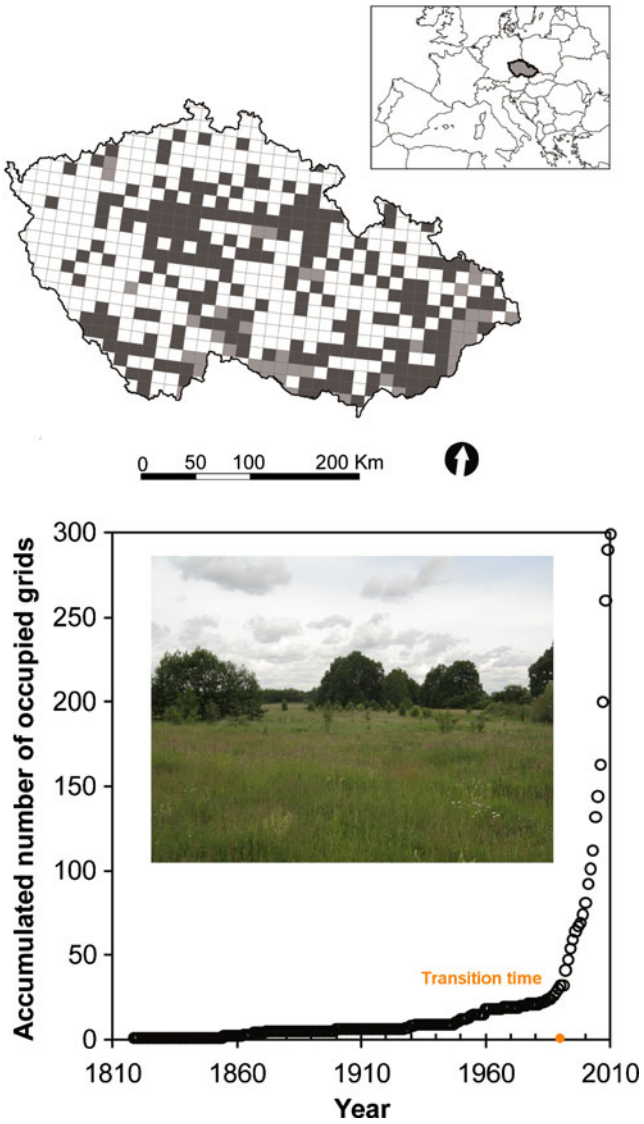

Fig. 1 Distribution and range expansion of the rose chafer beetle *O. funesta* in the Czech Republic. Grid cells on the *top map* show the occupancy of the species pre-1990 (*gray cells*) and post-1990 periods (*black cells*). The *bottom graph* presents the accumulated number of presence records from 1810 to 2010, with the *orange dot* indicating the transition time. The picture illustrates a typical riparian habitat (along river Tichá Orlice and between two ponds Velký and Malý Karlov) colonized by *O. funesta*

For the selection of key drivers of expansion, instead of using the above records of first occurrence, we calculated the colonization events of two consecutive decades as the dependent variable. For instance, for the pre-1990 decade, the status of a focal grid cell would be assigned to 1 if it was empty pre-1990 but occupied during 1990 to 2000; the value would be assigned to 0 if it remained empty at least till 2000. We ignored grid cells that were occupied before 1990 as the data is incapable of recording extinction events. Consequently, the dependent variable emphasizes the colonization event at a decadal pace, different from studies that use static presence/absence records as the dependent variable. This new dependent variable was then combined with various environmental variables grouped in five different categories (i.e., propagule pressure, climate, elevation, land use, and landscape structure) that could potentially play a role in explaining the species' extralimital colonization (Tables 1 and S2). Potential effects of sampling biases—due to unsystematic survey derived records—on the selection of environmental predictors were examined by means of a randomization procedure (described in the "Statistical analyses" subsection).

Data transformation

Propagule pressure (normally equally introduction effort) plays a key role in structuring natural communities and is also considered a key factor of invasion success (Richardson and Pyšek 2006; Catford et al. 2009; Lawrence and Cordell 2010). It depicts the effect of both the number and rate of incoming individuals dispersed from reachable populations on the colonization success of an empty habitat (Lockwood et al. 2005; Groom et al. 2006). The role of propagule pressure on establishment (i.e., colonization) is often tested using controlled experiments or records from acclimatization societies (Gertzen et al. 2011). We here propose a new way to quantify the LPP that could be important for successful colonization. For a focal grid cell (Fig. S1), we first calculated the number of presences (p_1) and absences (a_1) in the immediately adjacent cells ($n_1=p_1+a_1\leq 8$), and then the number of presences (p_2) and absences (a_2) in the secondary neighboring cells ($n_2=p_2+a_2\leq 16$). The LPP was then calculated as $\mathrm{LPP}=w_1(p_1/n_1)+w_2(p_2/n_2)$ ($0\leq \mathrm{LPP}\leq 1$), where w_1 and w_2 are weights. Specifically, we chose $w_1=2/3$ and $w_2=1/3$ to reflect that closer propagules contribute more to the colonization than propagules further away. Since LPP follows a binomial distribution, we performed a Logit transformation (Logit (LPP+0.01)) in the following analysis. Evidently, this definition not only considers the effect of local propagule size but also the spatial autocorrelation of existing propagules on the colonization of the focal cell.

To account for both the habitat preference of *O. funesta* and the spatial autocorrelation of environmental variables, we transformed all environmental variables in Table 1 as follows. Let x be the value of a specific variable in the focal grid cell, x_0 and x_1 be the mean values of the variable in empty and occupied adjacent cells, respectively; let x_3 and x_4 be the mean values of the variable in empty and occupied secondary neighboring cells. If the focal grid cell has been occupied during the period (i.e., the dependent variable is 1), we have the transformed variable $X=w_1(x-x_0)+w_2(x-x_3)$; if the focal cell remains empty (i.e., the dependent variable is 0), we have $X=w_1(x-x_1)+w_2(x-x_4)$. In this way, we considered both the spatial autocorrelation of the variable and the habitat

Table 1 Selected predictors, divided into categories and subcategories that potentially affected *O. funesta* occurrences

Categories	Subcategories	Predictors
Propagule pressure		Local propagule pressure
Climate		Annual mean temperature; mean and maximum summer temperature; total summer precipitation
Land use	Artificial surfaces	Artificial, nonagricultural vegetated areas (i.e., urban greenings)
	Agricultural areas	Pastures and meadows; heterogeneous agricultural areas
	Forest and seminatural areas	Scrub and/or herbaceous vegetation associations (i.e., seminatural vegetation)
	Wetlands	Inland wetlands
	Water bodies	Inland waters
Elevation		Mean; minimum; maximum; range and SD of elevation
Landscape structure	Patch density and size metrics	Number of patches; mean and median patch size; patch size coefficient of variance and SD
	Edge metrics	Total edge; edge density; mean patch edge
	Shape metrics	Mean shape index; area weighted mean shape index; mean perimeter–area ratio; mean patch fractal dimension; area weighted mean patch fractal dimension
	Diversity and interspersion metrics	Shannon's diversity and evenness indexes

preference of the species ($X>0$ indicates that the species prefers to colonize neighboring cells with a higher level of the variable). We then standardized these transformed variables in the following multivariate analyses.

Statistical analyses

To reduce multicollinearity among predictors, we calculated the variance inflation factors (VIFs; Belsley et al. 1980). The VIFs were computed for predictors in each study period (i.e., a decade before and after the transition time) using the R package HH (Heiberger and Holland 2004). All predictors with VIF≥2 were excluded from forthcoming analyses to avoid biases (Table S2; Graham 2003).

Generalized linear models (GLM) with a binomial distribution and Logit link function were computed for both study periods (decades before and after the transition time) using R (Lindsey 2000). For each period, we examined all model combinations of the finally selected predictors (i.e., 10 predictors, giving 1,023 model combinations) and then selected the best scenario based on the Akaike information criterion (AIC; Quinn and Keough 2002). When several models showed low AIC values, we calculated the difference in AIC values between the best and those models with a lower number of predictors (i.e., ΔAIC). Only models with ΔAIC≤2 received substantial support and were considered when making inferences (Burnham and Anderson 2002). Comparison of reduced deviance between models was computed using analysis of variance (ANOVA) with a chi-square distribution. If ΔAIC did not drop significantly ($P>0.05$), then we chose the model with fewer variables (Lindsey 2000). The same method was used to compare the final GLMs with the null model without any predictors (Šmilauer 2007).

In order to determine the variance explained of predictors in the final model, we applied a hierarchical partitioning method (Chevan and Sutherland 1991) using the R package hier.part (Walsh and MacNally 2003). The method of hierarchical partitioning can assess (1) independent contribution of a predictor, which is explained by the predictor itself exclusively; (2) joint contribution, which is shared with all other predictors; (3) total variance explained, which is a sum of the joint and independent contributions of each predictor; and (4) percentage of total variance explained, which gives the percentage of each predictor's total variance explained with respect to the sum of all predictors' total variance explained. A predictor with a negative joint contribution indicates that other predictors act as suppressors on the particular predictor (Walsh and MacNally 2003).

We applied a randomization procedure to examine the effect of potential sampling biases from nonsystematic surveys (Dennis et al. 1999) of *O. funesta* on the selection of key factors in the multivariate analyses. Specifically, a few years could have elapsed between the actual colonization and the detection of *O. funesta* (i.e., the first occurrence record) in a focal grid cell, and the time elapse between colonization and detection depends on multiple factors related to sampling effort and accessibility of the grid cell. For simplicity, we generated a random time elapse for each colonized grid cell following a Poisson distribution with a mean of 2 years. As currently absent cells could represent either nondetected pseudo-absences due to insufficient sampling effort or true absences (Hui et al. 2011), we chose a proportion of 5 % pseudo-absences and assigned these cells with the first occurrence year randomly selected from current colonized cells. We then performed the hierarchical partitioning for 1,000 runs following the previously

described randomization procedure, with each run including random corrections of the first occurrence year for both colonized and pseudo-absent cells.

Results

The accumulated records of first occurrences indicate a transition time from a slow increase of occupancy to a fast one around 1990, indicating a two-phase extralimital colonization event (Fig. 1). *O. funesta* occupied 32 grid cells till 1990 (with a 2 % annual increase of its occupancy), but then experienced a rapid occupancy increase and colonized another 48 new grid cells during the next decade after 1990 (with a 13 % annual increase of its occupancy; Table 2).

Consequently, we examined the changing role of LPP and other environmental variables in the colonization of *O. funesta* during the decade pre-1990 (from 1981 to 1990) and the decade post-1990 (from 1991 to 2000). Of the 31 environmental variables initially considered, 21 predictors were excluded due to multicollinearity (Table S2). Annual mean temperature was also excluded from the post-1990 GLM to facilitate comparisons with the pre-1990 model. The accuracy of this exclusion was confirmed using an ANOVA with a chi-square distribution, which did not show significant differences between the post-1990 GLMs with and without annual mean temperature (df=5; AIC=774.3; P=0.70). Most predictors included in the final analyses had a nonsignificant effect on the colonization.

During the pre-1990 decade (1981–1990), the colonization of *O. funesta* was facilitated by LPP, mean summer temperature, and area of inland waters. During the post-1990 decade (1991–2000), the colonization was positively driven by LPP, area of inland waters, and area of urban greenings (Table 3). The final selected models contained three predictors (Table S3) that had a significant and positive contribution in explaining the range expansion of *O. funesta* in both periods (Table 4) and one (seminatural vegetation) with negative contribution in the post-1990 period.

The results of the hierarchical partitioning of the final pre-1990 GLM showed that the independent contributions of the three predictors (LPP, mean summer temperature, and area of inland waters), expressed as proportions of total variance explained, were nearly the same. All predictors also shared low joint contribution to the proportion of variance explained (Σ<0.4 %; Fig. 2a). After 1990, the independent contribution of LPP rose nearly four times with respect to the previous period. The explained variance of area of inland waters was also much higher. The area of urban greenings had the highest independent contribution, while the joint contribution was higher for all land use predictors (area of inland waters, seminatural vegetation, and urban greenings). The joint contribution of LPP was extremely low and moved from positive to negative after 1990, indicating that land use predictors could act as weak suppressors (Fig. 2b).

We did not find any notable effects of potential sampling biases and uncertainty on the contribution of variables in the best selected GLM to the variance explained (as shown in Fig. 2) as, evidently, independent contribution of each variable in the best selected GLM was located within the 95 % confidence interval from 1,000 runs of the randomization test (Table S4), suggesting that our results are robust.

Discussion

Our study provides the first evidence of the population revival of *O. funesta* in Central Europe and how it has become one of the most common beetles in the region. The species experienced a two-phase extralimital colonization process—i.e., slow increase in occupancy until 1990, followed by a rapid increase in the next decade. Divergences in the rate of colonization pre-1990 and post-1990 respond to changes in the relevance of environmental variables. The best selected GLM explained merely 10.6 % variance of the colonization pre-1990, in contrast to 74.3 % variance explained post-1990 (Table 4), suggesting that our proposed method for data transformation is especially suitable for those species that experience fast changes in occupancy. The low variance explained for the early phase (pre-1990) could suggest that environmental tolerance and human-mediated dispersal played more important roles during the slow colonization than density-dependent propagule pressure and habitat preference.

Local propagule pressure

The extralimital colonization of *O. funesta* was clearly driven by the buildup of LPP, which has been long regarded as

Table 2 Summary statistics of transition time analysis with respect to the occurrence of *O. funesta* in the Czech Republic

Period	Y	R^2 (%)	F	P	Increase rate (yr^{-1})
Pre-1990	exp(−39.67+0.022×year)	95.0	3,044.50	*<0.01*	1.02
Post-1990	exp(−242.04+0.124×year)	97.0	541.70	*<0.01*	1.13

Significant P values appear in italics

Table 3 Summary results of the full GLMs explaining the distribution of *O. funesta* for the pre-1990 and post-1990 periods

Predictor	Pre-1990 period				Post-1990 period			
	Estimate	SE	*Z*	*P*	Estimate	SE	*Z*	*P*
Intercept	−1.25	0.54	−2.33	*0.02*	0.70	0.27	2.65	*<0.01*
Local propagule pressure	0.44	0.16	2.77	*0.01*	0.44	0.08	5.33	*<0.01*
Mean summer temperature	0.36	0.16	2.33	*0.02*	−0.02	0.09	−0.16	0.87
Urban greenings	0.16	0.10	1.61	0.11	0.98	0.21	4.65	*<0.01*
Pastures and meadows	−0.02	0.19	−0.09	0.93	−0.09	0.10	−0.94	0.35
Heterogeneous agricultural areas	0.04	0.17	0.26	0.80	0.04	0.10	0.37	0.71
Seminatural vegetation	0.07	0.20	0.38	0.70	−0.30	0.14	−2.17	*0.03*
Inland wetlands	0.16	0.12	1.27	0.20	0.11	0.10	1.15	0.25
Inland waters	0.25	0.11	2.24	*0.03*	0.61	0.15	3.99	*<0.01*
Mean perimeter–area ratio	−0.11	0.29	−0.38	0.71	−0.36	0.25	−1.44	0.15
Mean patch fractal dimension	−0.03	0.21	−0.12	0.90	−0.01	0.13	−0.10	0.92
AIC value	319.97				689.89			

Significant *P* values appear in italics and only predictors with VIF<2 were included

essential for establishing new colonies (MacArthur and Wilson 1967). If we divide the revival of *O. funesta* in the studied area into different invasion stages (transport, introduction, establishment, and spread; sensu Blackburn et al. 2011), the pre-1990 period can be considered as establishment and the post-1990 period can be considered as spread. Although propagule pressure has been considered a key factor for establishment success (Lockwood et al. 2005; Simberloff 2009), we here presented the first evidence of an even stronger effect of LPP on the last invasion stage (spread) of an extralimital species (or a domestic exotic species; Guo and Ricklefs 2010). The enhanced effect of LPP not only reaffirms the importance of propagule pressure in driving successful biological invasions, but also indicates the buildup of LPP to above certain thresholds as triggers for fast colonization and range expansion.

Climate change

Like most other flower-visiting rose chafers, *O. funesta* is a typical member of thermophilic fauna of Central Europe (Horion 1958; Balthasar 1956). It is, thus, not surprising that the mean summer temperature as an expression of ambient energy contributes to the climatic niche of the species. During the early phase of extralimital colonization before 1990, the species preferred to colonize those empty sites with high niche suitability. However, this effect of climate preference dwindled during the stage of fast colonization post-1990. As more suitable areas are being filled up at the fast colonization stage, the climate niche gradient between empty and colonized cells starts to disappear; consequently, this niche preference becomes undetectable (Ricklefs 2010). Although the future distribution of

Table 4 Summary results of the best selected GLMs explaining the distribution of *O. funesta* in the pre-1990 and post-1990 using an AIC selection procedure

Predictor	Pre-1990 period					Post-1990 period				
	Estimate	SE	*Z*	TVE	*P*	Estimate	SE	*Z*	TVE	*P*
Intercept	−1.32	0.53	−2.47	–	*0.01*	0.69	0.26	2.63	–	*<0.01*
Local propagule pressure	0.42	0.16	2.64	3.84	*<0.01*	0.44	0.08	5.47	13.26	*<0.01*
Mean summer temperature	0.35	0.15	2.36	2.96	*0.02*	–	–	–	–	–
Urban greenings	–	–	–	–	–	0.99	0.21	4.72	30.39	*<0.01*
Seminatural vegetation	–	–	–	–	–	−0.29	0.13	−2.24	5.66	*0.03*
Inland waters	0.28	0.11	2.65	3.78	*<0.01*	0.63	0.15	4.21	25.00	*<0.01*
AIC value	309.65					681.85				

Significant *P* values appear in italics

TVE total variance explained (in percent) derived from hierarchical partitioning

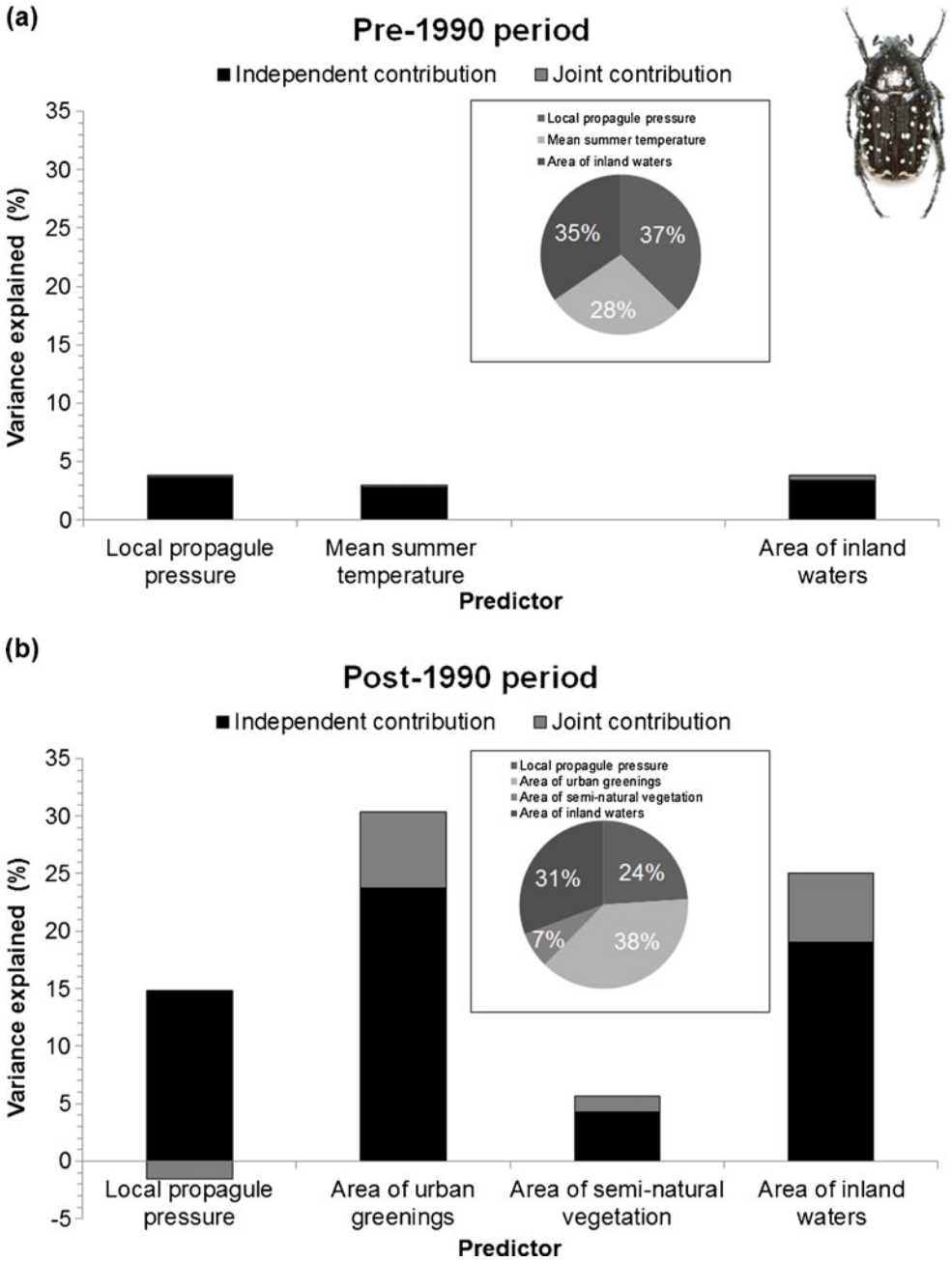

Fig. 2 Results of hierarchical partitioning showing the proportion of variance explained of selected predictors for *O. funesta* during the pre-1990 (**a**) and post-1990 (**b**) periods. The pie diagrams are the results of the independent contribution of predictors as a proportion of total explained variance

climatically suitable niches of the species is uncertain due to the recent rapid changes in climate (e.g., the gradual rise of the mean summer temperature in the Czech Republic from 15.5 °C in 1980 to 17.5 °C in 2000; Tolasz 2007), the result here suggests that the climate change will only play a trivial role in the fast extralimital colonization of rose chafer beetles in Central Europe.

Land use

The colonization of *O. funesta* was consistently facilitated by the existence of large areas of water courses and bodies in both study periods. Although many successful aquatic invaders spread through floods along riparian corridors (Skoglund 1989; Andow et al. 1990; Danvind and Nilsson 1997; Stohlgren et al. 1998), inland waters are often posed as a movement barrier for terrestrial species (see Lomolino et al. 2010 and references therein). Nevertheless, the evidence for terrestrial invertebrates seems to be highly fragmented (see Nève et al. 1996 for threatened butterfly or Ward 1987 for invasive ant). This becomes even more surprising as *O. funesta* was historically reported as relictual to xeric postglacial steppes (Horion 1958; Burakowski et al. 1983). The main reason for consistent effects of inland waters is probably the

potential increase of flowering plants along the banks and the presence of large amounts of decayed plant debris after floods. Species such as *O. funesta* can benefit from these resources by permitting adults to exploit the pollen of many plants and larvae to feed on decaying plant debris. It is also well-known that riparian corridors are important conservation structures that can facilitate the dispersal of fragmented populations (Fahrig and Merriam 1994). In the case of *O. funesta*, corridors—which fulfill an inherent need for movement (Simberloff et al. 1992)—may have acted as drift fences or greenways (Haddad and Baum 1999; Rosenberg et al. 1997).

Site-level management (e.g., in cities and reserves) often challenges the persistence of many insect taxa (Kadlec et al. 2008; Konvicka et al. 2008); however, our results show that the rose chafer beetles may respond well to intensive management. This is probably due to the positive changes of land use in surroundings (Tscharntke et al. 2002). Urban greenings like parks and gardens are known to host disparate insect communities (McIntyre 2000). The association of *O. funesta* with urban greenings during the rapid colonization suggests that a combination of nectar sources and compost heaps together with plant residues from mulching contributes significantly to the current revival of this species. *O. funesta* is known to visit many flowering plants and nectar sources from ornamental plants, which are (together with native plants) often used in urban gardens. Urban greenings, thus, keep a more continuous pool of flowers during the whole vegetation season than the natural environments that are more limited by climatic conditions; this is further supported by the negative response of *O. funesta* to the area of seminatural habitats. Furthermore, compost heaps are known to serve as refuges and stepping-stones for arthropods including invaders (Ødegaard and Tømmeras 2000).

Conclusion

O. funesta, the rose chafer beetle, which was rare in the Czech Republic in the past, is recently undergoing a rapid colonization event and has become one of the most common beetles in Central Europe. Our results suggested that this extralimital invader has shifted to a fast-spread phase after 1990, driven by the buildup of LPP and novel niches created by land use management. The colonization of *O. funesta* was facilitated by high summer temperatures in the slow establishment phase pre-1990 but not in the fast-spread phase post-1990. Instead, urban greenings and inland waters became important for fast colonization by providing sufficient food supply for adults and larval development. This is a timely reminder that species distribution modeling, in the framework of environmental changes, should fully acknowledge the changing role of these ecological and environmental factors at different stages of biological invasion.

Changes in the occupancy of a species not only offer the opportunity to elucidate the environmental drivers at play, but also manifest the need to constantly revise the conservation status of species. As the species is conspicuous and can hardly be overlooked (cf. Fisher 2011), the conservation status of *O. funesta* as a rare species in the Czech Republic evidently reflects the situation of the species before 1990 (Král 1989). In light of our findings, we suggest to pay more attention to the actualization of endangered species checklists, especially when they are part of the legal acts.

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